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Article in *Journal of Arid Environments* · January 2000

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The diet and nutrition of the Namaqua sandgrouse, an arid-zone granivore

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(Received 13 May 1998, accepted 14 July 1999)

The diet of the Namaqua sandgrouse, *Pterocles namaqua*, is described, and daily seed intake needed to meet limiting nutrient requirements during different stages of the annual cycle is estimated. Namaqua sandgrouse feed almost exclusively on seeds, mainly on those of protein-rich legumes. The energy content ($17\text{--}24\text{ kJ g}^{-1}$) of selected seed species is less variable than protein (10–37%) and amino acid (0.11–4.52%) content. Energy is usually the first limiting factor for adults, especially females producing eggs. Essential amino acids appear to be more limiting than energy for growing chicks, suggesting that chicks may be more dependent on protein-rich legume seeds than adults. The dietary requirements for essential amino acids in developing chicks are similar to those of females producing eggs, suggesting that chick development is the most nutritionally demanding stage in the annual cycle of Namaqua sandgrouse.

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Keywords: amino acid requirements; breeding; diet; granivory; nutrition;
Pterocles namaqua

Introduction

Sandgrouse (Pteroclididae) are highly specialized and successful inhabitants of the arid and semi-arid zones of Africa, the Middle East, and Asia (Thomas, 1984). The various species have a primarily granivorous diet, feeding mostly on the small, hard seeds of annual plants. Seeds are reported to be rich in energy and easily-metabolized carbohydrates, but are deficient in other essential nutrients, particularly proteins and essential amino acids (Wiens & Johnston, 1977). This has led to the assumption that large quantities of seeds are required to satisfy the energetic and nutritional needs of granivorous birds, particularly during periods of greatest nutrient demand. By feeding on the seeds of annual plants, which are produced super-abundantly in arid regions following suitable rainfall, and adopting a nomadic life style to track patches of high production, sandgrouse may be able to sustain high seed intake rates (Thomas, 1984). In addition, they may feed selectively on seeds with a high energy and/or protein content (Dixon & Louw, 1978; Thomas, 1984).

For most non-migratory birds, the physiological demands of reproduction are the most rigorous and critical within their annual cycle. Most species have therefore evolved the timing of breeding to coincide with the maximum availability of their species-specific food, particularly in strongly seasonal environments (Immelmann, 1973). Three of the four species of southern African sandgrouse, namely the double-banded sandgrouse (*Pterocles bicinctus*), Burchell's sandgrouse (*P. burchelli*) and the yellow-throated sandgrouse (*P. gutturalis*), breed primarily through the dry winter months, from April to September, when seed-food availability is high following seasonal late-summer rains (Skinner, 1996; Harrison *et al.*, 1997; Tarboton *et al.*, in press). The Namaqua sandgrouse (*P. namaqua*), on the other hand, does not necessarily breed when the food supply is optimal. This species has been observed to initiate breeding up to 5 months after seed production, with the breeding season extending into the start of the rainy season, when food availability can reach its lowest levels following seed germination (Lloyd *et al.*, in press *a*).

While there is a body of evidence detailing the diets of sandgrouse, no study has related the nutritional content of the seed species consumed to sandgrouse nutritional requirements during different stages of their annual cycle to identify potential bottlenecks. This paper examines the diet of the Namaqua sandgrouse and the nutritional content of its principal seed foods. Using published accounts of sandgrouse daily energy budgets (Hinsley, 1992; Hinsley & Ferns, 1994), and best estimates of the daily requirements for limiting nutrients, particularly essential amino acids, we construct daily energy and limiting nutrient requirement profiles for the Namaqua sandgrouse.

Methods

Diet

Crops were removed from 130 Namaqua sandgrouse collected at irregular intervals over the period 1993–1995. The total contents of each crop were removed, air-dried, and individually separated into the following fractions: grit, pebbles, different seed species, and other vegetable matter. Fractions were weighted to the nearest 0.01 g and the number of items counted. During the course of the study, seed and vegetative samples were collected from all flowering plants suspected of being consumed by Namaqua sandgrouse and, once identified, served as a reference collection for the identification of seeds found in sandgrouse crops.

Seed nutritional content and digestion efficiencies

The crude protein content of selected seed types was determined using the Kjeldahl procedure (A.O.A.C., 1975). The content of 16 amino acids in the selected seed types was determined using the method of McNab & Fisher (1984). The gross energy content of the selected seed types was determined using an adiabatic bomb calorimeter (A.O.A.C., 1975).

The efficiency of the digestive assimilation of 16 amino acids by Namaqua sandgrouse was determined using the following experimental procedure. Wild-caught Namaqua sandgrouse were housed in an aviary for 1 month with *ad libitum* access to water and lentil seed food. At the start of the experiment, four birds were moved to adjoining small wire cages (with no food, but free access to water) from 09 00 h on day 1. On day 2, each bird was fed 5 ml of a 50% (w/v) dextrose solution by means of a force-feeding tube that was long enough to reach the crop. This kept the birds in positive energy balance until the force-feeding of the test diet on day 3. Endogenous losses of amino acids from the digestive tract were determined by measuring amino acid

content of excreta collected between days 2 and 3. Five grams of the test diet (lucerne seed) were fed at 09 00 h on day 3 and trays were placed under the cages to collect all excreta voided. The voided excreta were collected at 09 00 h on day 5 and analysed for amino acid content as described above. The proportion of each amino acid assimilated by each bird was determined as:

$$(A - B - C)/A,$$

where A is the amino acid content of the 5 ml lucerne seed fed to the birds, B is the amino acid content of the excreta, and C is an adjustment for the endogenous losses from the digestive tract. The birds were then given *ad libitum* access to water and their normal diet for a week before the experiment was repeated on the same four birds.

Hinsley (1992) calculated the digestive efficiency of gross energy in the double-banded sandgrouse to be 0.76. The same is assumed to be true for the Namaqua sandgrouse.

Time budgets and daily energy expenditures

Hinsley (1992) and Hinsley & Ferns (1994) measured the resting metabolic rates (using open flow respirometry) of double-banded, black-bellied (*P. orientalis*) and pin-tailed sandgrouse (*P. alchata*). They then determined the energy expenditures of breeding and non-breeding birds using time budgets and estimates (based on previously published formulae or assumptions) of the relative energy costs of different activities. We obtained daily time budgets for non-breeding Namaqua sandgrouse in winter (June) from Lloyd *et al.* (in press *b*), and for breeding Namaqua sandgrouse in summer (November) from Lloyd *et al.* (in press *c*). We then estimated the daily energy budgets of breeding and non-breeding Namaqua sandgrouse in both winter (June) and summer (November) following the methodology employed by Hinsley & Ferns (1994), after making several assumptions based on the findings of Hinsley (1992) and Hinsley & Ferns (1994).

The arid-adapted double-banded (mean adult mass 189 g) and pin-tailed sandgrouse (mass 290 g) were found to have daytime resting metabolic rates (RMRs) 46% and 38% less than the allometric prediction of Aschoff & Pohl (1970) (Hinsley, 1992; Hinsley & Ferns, 1994). Low RMRs appear to represent an adaptation to desert life among birds (Dawson & Bennett, 1973; Dmi'el & Tel-Tzur, 1985; Hinsley *et al.*, 1993). We determined mean adult body masses from 845 Namaqua sandgrouse that were collected at irregular intervals from 1991–1995. Namaqua and double-banded sandgrouse are of equivalent adult body mass (180 g and 189 g, respectively), are largely sympatric in the arid and semi-arid habitats of southern Africa (Thomas & Maclean, 1981; Harrison *et al.*, 1997), and are equally adapted to hot desert conditions with respect to water and energy conservation and reduction of heat loads (Thomas & Maclean, 1981; Hinsley 1992). We therefore assume that Namaqua sandgrouse have RMRs 46% less than the allometric predictions of Ashoff & Pohl (1970):

$$\text{Predicted active phase (daytime) RMR} = 91 W^{0.729} \text{ in kcal day}^{-1}$$

$$\text{Predicted resting phase (night-time) RMR} = 73.5 W^{0.734} \text{ in kcal day}^{-1},$$

where W is weight in kg. Daytime RMRs are then 2.50 kJ h^{-1} (3.75 mW g^{-1}) for males and 2.40 kJ h^{-1} (3.81 mW g^{-1}) for females, while night-time RMRs are 2.00 kJ h^{-1} (3.01 mW g^{-1}) for males and 1.92 kJ h^{-1} (3.05 mW g^{-1}) for females.

The costs of thermoregulation were determined as excess metabolic heat production (H_m in mW g^{-1}) below a lower critical temperature of 32.0°C using the regression equation:

$$H_m = 9.65 - 0.187 T_c \text{ (Hinsley, 1992),}$$

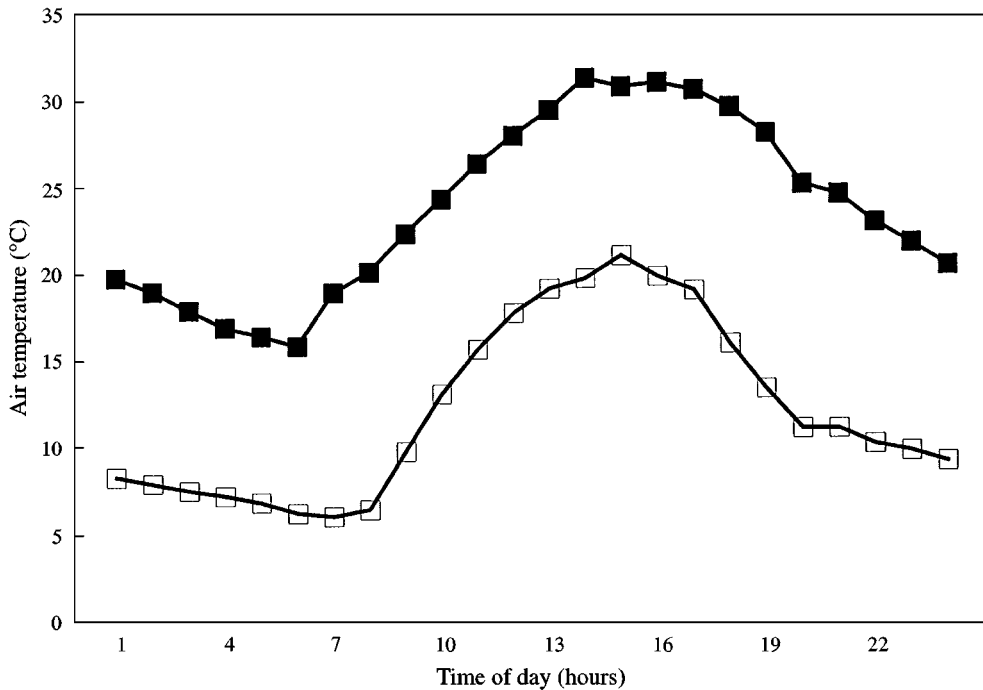


Figure 1. Average hourly air temperatures measured at Upington weather station for the months of November (summer) (—■—) and June (winter) (—□—) 1994.

where T_c = operative temperature for a bird in direct sunlight at ground level. By comparing mean hourly air temperature, from monthly means (for 1994) measured at Upington weather station (Fig. 1), to air, ground, and operative temperatures recorded in Hinsley & Ferns (1994), a number of assumptions were made with regard to operative temperatures experienced by an incubating sandgrouse. Operative temperatures were assumed to exceed the assumed lower critical temperature (32°C) between 08 00 h and 19 00 h during November, and between 14 00 h and 16 00 h during June. Outside of these hours, operative temperature was assumed to equal ambient air temperature.

Hinsley & Ferns (1994) assigned a separate cost to each daytime activity: foraging, preening, standing alert, and walking. The average cost of all these activities considered together, for both male and female pin-tailed sandgrouse, during both the non-breeding season and while caring for chicks during the breeding season, was $1.5 \times \text{RMR}$. As we did not determine detailed time budgets for Namaqua sandgrouse, we assumed that the cost of these activities (considered together) was $1.5 \times \text{RMR}$ for both males and females while not breeding, and for males during the breeding season. Because females had limited time to feed during the incubation period, we assumed that they foraged continuously during daylight hours when not incubating or flying, with an energetic cost of foraging of $2 \times \text{RMR}$ (Ferns *et al.*, 1979). The cost of flying was assumed to be $13 \times \text{daytime RMR}$ (Hinsley & Ferns, 1994).

At operative temperature above 32°C , the cost of incubation was assumed to be $1.3 \times \text{RMR}$ (daytime), due to some movement on the nest by the incubating bird (Hinsley & Ferns, 1994). At operative temperatures below 32°C , the cost of incubation was considered to be additive to RMR and was calculated using equation 5.53 of Kendeigh *et al.* (1977):

$$H_{\text{inc}} = n \times w \times h \times b(T_{\text{egg}} - T_{\text{nest}})(1 - c),$$

where H_{inc} is the heat supplied to the eggs in kJ h^{-1} , n is the clutch size (3), w is the mean egg weight during incubation (10.1 g; Thomas & Maclean, 1981), h is the specific heat capacity of eggs ($0.003 \text{ kJ g}^{-1} \text{ }^\circ\text{C}^{-1}$; Ashkenazie & Safriel, 1979 quoting D.W. Norton, unpubl. Ph.D. thesis, University of Alaska), b is the cooling rate of the eggs ($2.48 \text{ }^\circ\text{C h}^{-1} \text{ }^\circ\text{C}^{-1}$, predicted from egg weight; Kendeigh *et al.*, 1977), T_{egg} is egg temperature ($30 \text{ }^\circ\text{C}$; Caldwell & Cornwell, 1975; Walsberg & Voss-Roberts, 1983), T_{nest} is nest air temperature ($31.9 \text{ }^\circ\text{C}$ by day and $28.5 \text{ }^\circ\text{C}$ at night; Caldwell & Cornwell, 1975), and c is the fraction of the egg in contact with the brood patch (0.3). H_{inc} was then 1.18 kJ h^{-1} at night and 0.65 kJ h^{-1} during the day. The cost of incubation was then assumed to be $H_{inc} + (1.3 \times \text{RMR})$ during daytime operative temperatures below $32 \text{ }^\circ\text{C}$, and $H_{inc} + \text{RMR}$ at night.

Additional energy requirements for egg production

Whole-egg energy densities of the eggs of precocial species average 7.76 kJ g^{-1} wet mass (Walsberg, 1983). Each 11.1 g Namaqua sandgrouse egg (Thomas & Maclean, 1981) is therefore assumed to contain 86.12 kJ energy. The digestive efficiency of gross energy was taken to be 0.76 (Hinsley, 1992) and the efficiency of energy deposition as protein in eggs was taken to be 0.75 (Walsberg, 1983). Dietary energy requirements then equate to 151.12 kJ per egg, or 453.35 kJ for a clutch of three. The length of the rapid follicular growth phase (T_{RG}) in the Namaqua sandgrouse was calculated using the equation:

$$T_{RG} = 2.96 \times M_E^{0.278} \text{ (Walsberg, 1983),}$$

where M_E = egg mass in grams (11.1 g for Namaqua sandgrouse) and T_{RG} computes to 5.8 days. With a laying interval of 2 days and a clutch size of three eggs (Lloyd *et al.*, in press *c*) the nutritional costs of producing a full clutch are therefore estimated to be spread over a total period of approximately 10 days in this species.

Amino acid requirements for daily maintenance and egg production

The dietary amino acid requirements for daily maintenance and egg production in the laying hen, as reported by McDonald & Morris (1985), are summarized in Table 1. For the purposes of this study, Namaqua sandgrouse are assumed to have equivalent nutritional requirements per unit weight. The dietary amino acid requirements for individual amino acids (AA in mg) to produce a clutch of three Namaqua sandgrouse eggs (11.1 g each) were calculated as:

$$AA_E = CR_E \times 11.1 \times 3,$$

where CR_E is the coefficient of response (see Table 1) for the particular amino acid being considered. The two sulphur amino acids (SAAs) cysteine and cystine (hereafter referred to collectively as cyst(e)ine) can be synthesized from the other SAA, methionine. The daily requirement for methionine was therefore considered under two scenarios; a requirement to meet methionine needs alone, and a requirement to meet total SAA requirements (i.e. to compensate for cyst(e)ine deficiencies). Again, these nutritional requirements are assumed to be spread over approximately 10 days.

Nutritional requirements for chick growth

A Gompertz growth model (Brown & Rothery, 1993, pp. 48–51) was fitted to growth (daily weight) data, kindly supplied by Shelley Hinsley, for six captive-reared (four

Table 1. Dietary amino acid requirements (also referred to as the coefficients of response) for daily maintenance (mg amino acid per kg body weight per day) and egg production (mg amino acid per g egg output) in the laying hen (McDonald & Morris, 1985), and the amino acid contents of body and feather proteins (g amino acid per kg protein) in the turkey *Meleagris gallopavo* (Emmans, 1989). Cyst(e)ine = cysteine + cystine. SAA = sulphur amino acids (methionine and cyst(e)ine)

Amino acid	Daily maintenance CR _M (mg kg ⁻¹ d)	Egg production CR _E (mg g ⁻¹ egg)	Body protein CR _{BP} (g kg ⁻¹)	Feather protein CR _{FP} (g kg ⁻¹)
Arginine	53	8.9	68	65
Histidine	16	3.3	26	8
Isoleucine	67	7.97	40	40
Leucine	32	12.5	71	70
Lysine	73	9.99	75	18
Phenylalanine	16	7.6	40	45
Threonine	32	6.9	42	44
Tryptophan	11	2.62	10	7
Valine	76	8.9	44	60
Methionine	31	4.77	25	6
Cyste(e)ine	49	3.53	11	70
SAA	80	8.3	36	76

hand-reared together and two raised together by double-banded sandgrouse surrogate parents) pin-tailed sandgrouse chicks. Assuming a similar growth rate for Namaqua sandgrouse chicks (proportional to an average adult weight of 180 g), curves of growth (daily weight) and daily weight gain were plotted for a hypothetical Namaqua sandgrouse chick. After calculating the instantaneous growth rates (G in grams), the daily body protein (BP), and feather protein (FP) gains for a 19-day old (time $t = 19$) Namaqua sandgrouse chick were determined using the expressions:

$$BP_t = 0.18 \times G_t \text{ (Emmans, 1989), and}$$

$$FP_t = BP_t^{1.21} \text{ (Emmans, 1989).}$$

The total dietary amino acid requirements of a 19-day old chick were then determined as:

$$DR = AA_M + AA_{BP} + AA_{FP} = (CR_M \times W_{t_B}) + [(CR_{BP} \times W_{t_{BP}})/c] + (CR_{FP} \times W_{t_{FP}}/c),$$

where AA_M is the amino acid required for maintenance, AA_{BP} is the amino acid required to produce body protein growth, AA_{FP} is the amino acid required to produce feather protein growth, CR are the coefficients of response (see Table 1) for maintenance, body protein growth and feather protein growth, and c is the efficiency of amino acid assimilation from the diet (0.8; Emmans, 1989).

Daily seed intake

The daily intake (DI in grams) of the various seed types (considered alone) required to meet the daily dietary amino acid requirements (DR in grams) during different developmental stages was determined using the expression:

$$DI = DR/(SC/100),$$

where SC is the amino acid content of the particular seed type (from Table 2). The daily seed intake to meet daily dietary energy requirements was determined by dividing dietary requirements by the gross energy content of the particular seed type (from Table 2). The intake needed to meet the requirements for the first limiting amino acid was then compared to the intake needed to meet energy requirements, to determine which was more limiting.

Results

Diet

Namaqua sandgrouse consumed the seeds of a wide variety of plants (Table 2), with all but two of the plant species being annuals. The two principal seed-plant families were the Fabaceae and Aizoaceae, comprising 57% and 20% of the diet (by weight), respectively. Leaves and fruit comprised <1% of the diet, and no animal remains were found in 130 crops. Small quantities of pebbles and grit were usually present in the diet. A single week-old chick collected in the late afternoon in the Langberg had a crop full of the same seeds as adult sandgrouse in that area were feeding on. Depending on the size of the seeds, a full crop contained between 3000 and 40,000 seeds. The seeds of a single species usually comprised more than 50% of an individual bird's crop contents by weight or item numbers (Fig. 2). The crop seed contents of birds collected in the late afternoon (i.e. at the end of the day's feeding) averaged 8.24 g (Table 3), and the largest volume for a full crop of seeds was 23.5 ml (from a female).

Table 2. Gross energy (GE), crude protein and amino acid content of selected Namaqua sandgrouse seed food species. The first four species are legumes

Seed species	GE (kJ g ⁻¹)	Protein (%)	Amino acid (% of dry mass)														Recovery (%)				
			Ala	Arg	Asp	Cys	Glu	Gly	His	Ile	Leu	Lys	Met	Phe	Pro	Ser		Thr	Tyr	Val	
<i>Requena</i>	21.09	37.37	1.65	3.67	4.52	0.37	7.92	1.79	1.23	1.61	3.23	2.33	0.39	2.02	2.01	1.76	1.23	0.73	1.96	95.92	
<i>sphaerosperma</i>																					
<i>Lucerne</i>	19.69	31.71	1.39	3.10	3.64	0.34	5.85	1.88	0.99	1.42	2.41	2.65	0.43	1.50	1.61	1.41	1.20	1.01	1.67	95.01	
0																					
<i>Tephrosia</i>	19.17	34.21	1.46	2.64	4.04	0.27	6.68	1.60	0.97	1.52	2.98	2.53	0.38	1.89	2.00	1.70	1.15	0.87	1.71	95.00	
<i>burchelli</i>																					
<i>T. dregeana</i> *	21.03	32.00																			
<i>Lineum</i>	17.79	9.81	0.46	1.20	0.87		1.79	0.80	0.31	0.43	0.74	0.43	0.14	0.44	0.45	0.44	0.40	0.18	0.66	94.96	
<i>arenicolum</i>																					
<i>Cleome</i> sp.	23.93	18.60	0.86	1.78	1.67	0.44	3.53	1.16	0.51	0.85	1.23	0.94	0.25	0.79	1.03	0.53	0.60	0.39	1.32	95.02	
<i>C. diandra</i> *	21.18	16.00																			
<i>C. luederitzian</i> *	21.48	16.00																			
<i>Cyperaceae</i>	17.17	10.50	0.47	1.16	1.04	0.11	1.97	0.52	0.26	0.44	0.84	0.41	0.34	0.60	0.48	0.44	0.36	0.27	0.72	95.00	
<i>unid.sp.</i>																					
<i>Gisekia/</i>	20.01	15.82	0.7	3.62	1.38	0.14	2.7	1.24	0.76	0.6	0.97	1.01	0.38	0.56	0.78	0.68	0.51	0.61	0.79	94.99	
<i>Chenopodium</i> †																					

*From Dixon & Louw (1978).

†A 1:1 mix by volume of the two seed species.

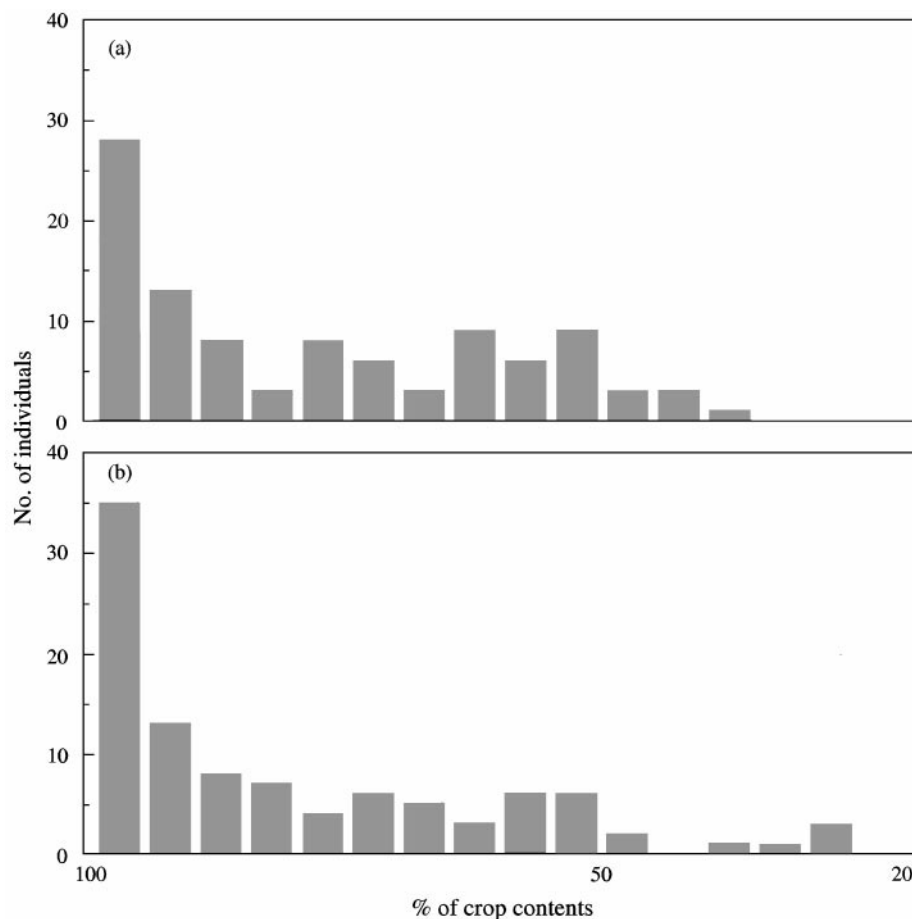


Figure 2. The frequencies and the proportional contribution of the dominant seed species in the crop by (a) weight and (b) item totals ($n = 100$). The identity of the dominant seed species is variable between individuals. Only crop samples containing at least 1 g of seed were considered in the analysis.

Seed nutritional content and amino acid digestibilities

The nutritional content of selected seed species is summarized in Table 2. Legume species (family Fabaceae) generally had more than twice the amount of crude protein (31.7–37.4%) than non-legume species (9.8–18.6%). Gross energy content was less variable between seed species (17–24 kJ g⁻¹). Amino acid digestibilities averaged 0.81 for asparagine, but ranged from 0.95 to 0.99 for all the others, and averaged 0.97 for all amino acids considered together.

Daily time and energy budgets

The mean adult body mass of Namaqua sandgrouse, which is significantly different between the sexes ($t_{843} = 10.18$, $p < 0.001$), was 184.7 g for males (S.D. = 13.2, $n = 548$) and 174.8 g for females (S.D. = 13.9, $n = 297$; excluding females with well developed ovary follicles [> 5 mm in diameter] or eggs in the oviduct). The estimated daily time and energy budgets of both breeding and non-breeding Namaqua sandgrouse

Table 3. *The average weights (g) of crop seed contents from Namaqua sandgrouse adults collected in the late afternoon at either Droëgrond or the Langberg at different times of the year*

Locality	Date	Mean \pm S.D.	<i>n</i>	Range
Droëgrond	23 Nov 1993	8.30 \pm 0.91	3	7.27–8.98
Droëgrond	02 May 1994	6.26 \pm 1.16	10	4.55–8.33
Langberg	12 May 1994	9.09 \pm 1.19	13	7.01–10.88
Langberg	01 Aug 1994	7.60 \pm 1.51	17	4.79–9.22
Droëgrond	15 Aug 1994	9.14 \pm 3.27	6	4.05–12.32
Droëgrond	17 March 1995	9.36 \pm 1.77	15	6.12–13.99
Langberg	22 March 1995	4.92 \pm 1.88	6	3.15–7.88
Langberg	12 July 1995	10.40 \pm 1.06	8	8.73–11.90
		8.24 \pm 2.20	78	3.15–13.99

are summarized in Table 4. The energy budgets of nesting males are 12–14% higher than those of non-resting males, but roughly equivalent between nesting and non-nesting females. The cost of thermoregulation was nearly three times higher in winter than in summer. Due to the high costs of flying, daily energy budgets are sensitive to the length of time spent flying each day.

Nutritional requirements for chick growth

The Gompertz growth model fitted to the pin-tailed sandgrouse growth data ($W_t = 224 \times \exp[-3.466(\exp(-0.0667t))]$; Table 5 and Fig. 3) accounted for 98.5% of the variance. For the growth curves fitted to the six individual chicks, mature weight (W_m) ranged between 162.7 and 301.5 g, but averaged 224.4 g, and the rate of maturing (B , per day) ranged between 0.0393 and 0.0678, averaging 0.0667. Daily weight gain in a hypothetical Namaqua sandgrouse chick peaks at 3.43 g at an age of approximately 19 days (Fig. 3).

Daily seed intake

Daily seed intakes needed to meet the estimated daily energy requirements of Namaqua sandgrouse vary relatively little between seed species (Table 6), and range from 5.85–11.35 g day⁻¹ for non-breeding birds, to 6.66–12.64 g day⁻¹ for nesting birds, to 7.49–13.73 g day⁻¹ for females producing eggs.

For birds not producing eggs, dietary energy requirements are first limiting in all seed-food species. In females producing eggs, the daily dietary requirement for the amino acids methionine or lysine are more limiting than energy in some seed species. Energy budgets were not determined for a developing chick, but an appraisal of seed intakes required to meet limiting amino acids (Table 7) suggests that amino acids may usually be more limiting than energy. For females producing eggs and developing chicks, lysine is the first limiting amino acid in the unidentified species of Cyperaceae, and methionine is first limiting in all other seeds tested (Table 8).

Discussion

From the dietary analysis, it can be concluded that Namaqua sandgrouse feed almost exclusively on seeds, and mainly those of annual leguminous plants (Table 8). In most

Table 4. Time and energy budgets of breeding and non-breeding Namaqua sandgrouse at Droëgrond during summer and at Prynnsberg during winter

Activity	Summer (November)*				Winter (June)†			
	Breeding Male	Breeding Female	Non-breeding Male	Non-breeding Female	Non-breeding Male	Non-breeding Female	Breeding Male	Breeding Female
Night inactivity	—	10h15min 19.73 kJ	10h15min 20.54 kJ	10h15min 19.73 kJ	13h40min 27.39 kJ	13h40min 26.31 kJ	—	13h40min 26.31 kJ
Night incubation	10h15min 32.68 kJ	—	—	—	—	—	13h40min 43.57 kJ	—
Day activity	9h50min 36.91 kJ	35min 2.10 kJ	13h20min 50.05 kJ	13h20min 48.08 kJ	9h35min 35.97 kJ	9h35min 34.56 kJ	5h20min 20.02 kJ	35min 2.10 kJ
Foraging	—	3h15min 15.63 kJ	—	—	—	—	—	2h55min 14.02 kJ
Day incubation	4h15min 15.61 kJ	9h30min 29.69 kJ	—	—	—	—	4h15min 16.58 kJ	6h05min 22.95
Thermoregulation	22.32 kJ	21.73 kJ	22.32 kJ	21.73 kJ	60.29 kJ	55.93 kJ	60.29 kJ	55.92 kJ
Flying	25min 13.54 kJ	25min 13.00 kJ	25min 13.54 kJ	25min 13.00 kJ	45min 24.38 kJ	45min 23.40 kJ	45min 24.38 kJ	45min 23.40 kJ
DEE	121.06 kJ	101.88 kJ	106.45 kJ	102.54 kJ	148.03 kJ	140.20 kJ	164.84 kJ	144.71 kJ

*Time budgets obtained from Lloyd et al. (in press c)

†Time budgets obtained from Lloyd et al. (in press c)

Table 5. The growth rates of pin-tailed sandgrouse chicks (P-tS), the Gompertz model fitted to the pin-tailed sandgrouse data and the estimated growth rates of Namaqua sandgrouse chicks (NS)

Age (d)	Average P-tS weights (g)*	Gompertz model P-tS weights (g)	Gompertz model NS weights (g)	Instantaneous NS weight gain (g d ⁻¹)†	NS body protein weight gain (g d ⁻¹)‡	NS feather protein weight gain (g d ⁻¹)‡
1	13.80	8.75	5.43	1.18	0.213	0.038
3	18.60	13.12	8.15	1.55	0.279	0.053
6	29.15	21.95	13.63	2.12	0.382	0.078
8	35.30	29.34	18.21	2.48	0.447	0.094
10	44.40	37.82	23.45	2.80	0.504	0.109
12	60.55	47.23	29.32	3.06	0.551	0.122
14	66.25	57.37	35.62	3.25	0.586	0.131
16	70.80	68.02	42.23	3.38	0.608	0.137
17	77.03	73.46	45.60	3.41	0.614	0.139
18	84.25	78.94	49.01	3.43	0.617	0.139
19	85.58	84.44	52.42	3.43	0.618	0.140
20	90.70	89.93	55.83	3.42	0.615	0.139
21	94.93	95.39	59.22	3.92	0.611	0.138
22	99.98	100.80	62.58	3.35	0.604	0.136
23	97.50	106.14	65.89	3.30	0.595	0.133
24	109.33	111.39	69.15	3.24	0.584	0.130
26	115.68	121.56	75.47	3.10	0.558	0.123
28	129.55	131.22	81.46	2.93	0.527	0.115
30	137.73	140.31	87.11	2.74	0.493	0.106
31	143.23	144.62	89.78	2.64	0.475	0.102
36	154.50	163.79	101.68	2.14	0.386	0.079
42	180.50	181.69	112.80	1.59	0.287	0.055
53	214.00	202.74	125.84	0.85	0.154	0.026

*Measurements from six individuals.

†Calculated as $0.18 \times \text{body weight gain}$ (Emmans, 1989).

‡Calculated from: feather protein = (body protein)^{1.21} (Emmans, 1989).

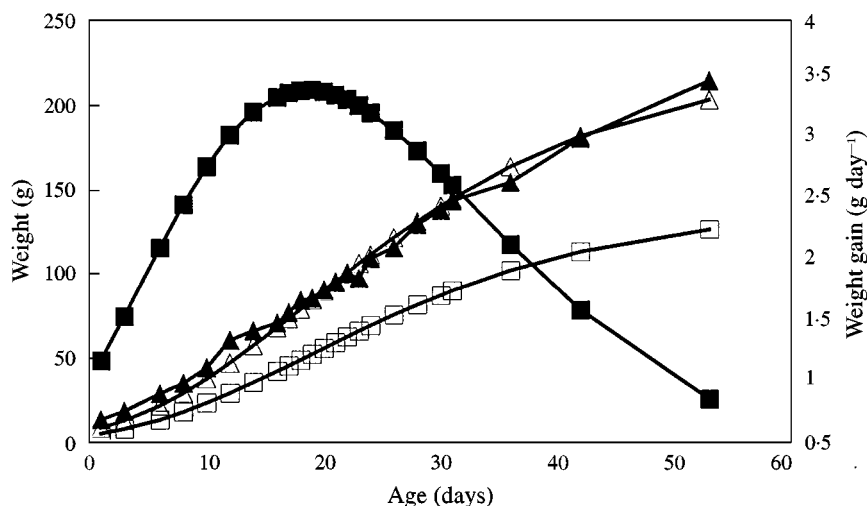


Figure 3. Observed and Gompertz-modelled growth curves for pin-tailed (P-tS) and Namaqua sandgrouse (NS) chicks. Weight measurements were averaged for six pin-tailed sandgrouse chicks reared in captivity. P-tS measured weights (—▲—), NS modelled Gompertz growth (---□---), P-tS fitted Gompertz growth curve (—△—), NS estimated weight gain (—■—).

individuals sampled, the seeds of a single species comprised more than 50% (and commonly more than 95%) of crop seed contents by weight or item numbers (Fig. 2). This suggests that individuals are either highly selective in what they eat, or that they feed in localized patches where only the seeds of single species predominate. Soil

Table 6. Daily seed intakes (grams) of different seed types (considered alone) required to meet daily energy requirements in male and female Namaqua sandgrouse during summer and winter breeding and non-breeding seasons, and during the 10-day egg production period (EP) in females. See Table 8 for full names of seed species

Seed species	Summer non-br.	Winter non-br.	Summer breeding	Winter breeding	EP alone	Summer br. + EP	Winter br. + EP
Males							
<i>Requernia</i>	6.64	9.23	7.55	10.28	—	—	—
<i>Tephrosia</i>	7.31	10.16	8.31	11.32	—	—	—
<i>Limeum</i>	7.87	10.95	8.96	12.19	—	—	—
<i>Cleome</i>	5.85	8.14	6.66	9.06	—	—	—
Cyperaceae	8.16	11.35	9.28	12.64	—	—	—
<i>Gis./Chen.</i>	7.00	9.73	7.96	10.84	—	—	—
Females							
<i>Requernia</i>	6.40	8.75	6.36	9.03	2.15	8.51	11.18
<i>Tephrosia</i>	7.04	9.62	6.99	9.93	2.37	9.36	12.30
<i>Limeum</i>	7.59	10.37	7.54	10.70	2.55	10.09	13.25
<i>Cleome</i>	5.64	7.71	5.60	7.96	1.89	7.49	9.85
Cyperaceae	7.86	10.75	7.81	11.09	2.64	10.45	13.73
<i>Gis./Chen.</i>	6.74	9.22	6.70	9.52	2.27	8.97	11.79

Table 7. Daily seed intakes (grams) of different seed types (considered alone) required to meet daily amino acid requirements for maintenance and during the 10-day egg production period in female Namaqua sandgrouse, and for maintenance and growth in a 19-day old chick. SAA = methionine requirement to meet total SAA requirements (i.e. to compensate for cyst(e)ine deficiencies). First limiting amino acid component in bold type. See Table 1 for full amino acid names and Table 8 for full names of seed species

Seed species	Amino acids											
	Arg	His	Ile	Leu	Lys	Phe	Thr	Tyr	Val	Cys	Met	SAA
	Daily maintenance requirements											
Requemia	0.25	0.23	0.73	0.17	0.55	0.14	0.45	0.26	0.68	2.32	1.38	(1.84)
Tephrosia	0.35	0.29	0.77	0.19	0.51	0.15	0.49	0.22	0.78	3.24	1.45	(2.19)
Limeum	0.77	0.92	2.74	0.76	2.94	0.64	1.42	1.09	2.02	-	3.9	-
Cleome	0.52	0.55	1.39	0.45	1.36	0.35	0.94	0.5	1.01	1.96	2.14	(2.03)
Cyperaceae	0.80	1.09	2.65	0.67	3.11	0.47	1.54	0.7	1.85	8.09	1.59	(3.12)
Gls./Chen.	0.26	0.37	1.96	0.58	1.26	0.5	1.1	0.32	1.68	6.26	1.41	(2.69)
	Daily egg production requirements (alone)											
Requemia	0.81	0.89	1.65	1.29	1.43	1.26	1.86	1.19	1.52	3.18	4.05	(3.63)
Tephrosia	1.12	1.13	1.74	1.40	1.32	1.34	2	1	1.73	4.44	4.24	(4.32)
Limeum	2.47	3.59	6.2	5.64	7.67	5.78	5.82	4.93	4.51	-	11.40	-
Cleome	1.67	2.15	3.14	3.38	3.55	3.2	3.86	2.26	2.24	2.69	6.25	(4.00)
Cyperaceae	2.56	4.29	6	4.96	8.09	4.22	6.31	3.18	4.12	11.09	4.64	(6.17)
Gls./Chen.	0.82	1.46	4.43	4.3	3.29	4.51	4.51	1.44	3.75	5.58	4.14	(5.30)
	Daily maintenance + egg production requirements											
Requemia	1.06	1.12	2.38	1.46	1.98	1.39	2.32	1.46	2.2	5.49	5.44	(5.46)
Tephrosia	1.48	1.42	2.51	1.59	1.82	1.49	2.49	1.22	2.51	7.67	5.68	(6.51)
Limeum	3.25	4.51	8.94	6.4	10.6	6.42	7.23	6.02	6.54	-	15.33	-
Cleome	2.19	2.7	4.53	3.84	4.91	3.55	4.79	2.76	3.25	4.65	8.39	(6.03)
Cyperaceae	3.36	5.39	8.66	5.63	11.20	4.68	7.85	3.89	5.96	19.18	6.23	(9.29)
Gls./Chen.	1.08	1.83	6.39	4.87	4.56	5.01	5.61	1.76	5.44	14.84	5.55	(7.99)
	Daily maintenance and growth in a 19-day old chick											
Requemia	1.82	1.75	2.37	2.08	2.63	1.92	3.26	1.23	2.29	5.64	5.22	(5.42)
Tephrosia	2.53	2.22	2.5	2.26	2.43	2.05	3.5	1.03	2.61	7.88	5.45	(6.46)
Limeum	5.56	7.03	8.9	9.1	14.12	8.86	10.18	5.07	6.8	-	14.72	-
Cleome	3.75	4.21	4.51	5.45	6.54	4.9	6.75	2.33	3.38	4.78	8.05	(5.98)
Cyperaceae	5.75	8.41	8.62	8	14.91	6.46	11.05	3.28	6.21	19.69	5.98	(9.22)
Gls./Chen.	1.84	2.85	6.36	6.93	6.07	6.91	7.90	1.48	5.66	15.24	5.33	(7.93)

Table 8. The total crop contents as a proportion of 1,220,640 items weighing 777.98g from 130 Namaqua sandgrouse collected at Dröëgrond (29° 07' S 20° 16' E; n = 57), the Langberg (28° 44' S 22° 09' E; n = 58), Tontelbos (30° 56' S 20° 23' E; n = 7), Papkuil (32° 28' S 19° 39' E; n = 6), Bulletrap (29° 28' S 17° 46' E; n = 1), and Graaf-Reinet (32° 24' S 24° 35' E; n = 1) through the course of the study

Seed family	Seed species	% Items	% Weight
Fabaceae	<i>Indigofera alternans</i>	22.47	21.11
	<i>Lotononis</i> spp.	1.84	1.69
	<i>Melolobium candicans</i>	0.16	1.81
	Unidentified sp. 1	0.01	0.05
	<i>Requernia sphaerosperma</i>	4.62	24.27
	<i>Tephrosia burchelli</i>	0.22	1.89
	<i>Cassia italica</i>	0.08	2.47
	<i>Acacia</i> sp.	<0.01	0.04
	Unidentified sp. 2	1.32	1.57
	<i>Medicago laciniata</i>	<0.01	<0.01
	<i>Cullen obtusifolia</i>	<0.01	0.02
Aizoaceae	<i>Limeum aethiopicum</i>	0.55	1.05
	<i>Limeum africanum</i>	6.78	6.39
	<i>Limeum arenicolum</i>	1.65	4.10
	<i>Limeum viscosum</i>	0.29	0.78
	<i>Gisekia pharnacioides</i>	23.70	7.64
	<i>Trianthema triquetra</i>	0.03	0.02
	<i>Hypertelis salsoloides</i>	<0.01	<0.01
Amaranthaceae	<i>Amaranthus</i> spp.	7.32	4.69
Sterculiaceae	<i>Hermannia</i> spp.	0.14	0.19
Pedaliaceae	<i>Sesamum triphyllum</i>	0.17	0.33
Capparaceae	<i>Cleome</i> sp.	0.12	0.08
Zygophyllaceae	<i>Tribulus</i> spp.	0.35	1.57
Chenopodiaceae	<i>Chenopodium</i> sp.	14.24	6.70
Cyperaceae	Unidentified spp.	13.42	6.33
Euphorbiaceae	<i>Chamaesyce inaequilatera</i>	0.02	0.02
Lamiaceae	Unidentified sp.	0.02	0.04
Acanthaceae	Unidentified sp.	0.17	0.37
Poaceae	<i>Triticum</i> sp.	0.04	1.36
	Unidentified sp.	<0.01	<0.01
Unidentified	Unidentified spp.	0.17	0.71
Leaves/fruits		0.01	0.03
Pebbles		0.06	1.73
Grit			0.85

sampling of the seed banks at localized sandgrouse feeding sites often found that single seed species predominated due to the patchiness of germination and growth in different plant species (Lloyd *et al.*, in press *a*). The ability of the birds to feed selectively should not be discounted though, particularly in view of the differences in nutritional value of different seed species (Table 2). Furthermore, *Limeum arenicolum* and *L. viscosum* seeds often occurred at high densities at both the Langberg and Dröëgrond, but were generally avoided unless other seeds were in short supply (Lloyd

et al., in press a). *Limeum arenicum* seed was the least nutritious of the species analysed in terms of both energy and limiting amino acid availability.

As expected, the protein-rich legume species were generally far richer in amino acids than non-legumes (Table 2). The only exception occurred with the amino acid methionine; *Gisekia pharnacioides*/*Chenopodium* sp. mix and the unidentified species (Cyperaceae) are all non-leguminous and not particularly rich in protein, but are equally as rich in methionine as legumes. Legume seeds are a dominant component of the diet in most sandgrouse species whose diet has been studied in any detail (Cramp *et al.*, 1985; Johnsgard, 1991). This has generally been ascribed to the higher protein content of these seeds relative to non-leguminous seeds, a conclusion supported by the results of this analysis.

The Namaqua sandgrouse appears to digest the amino acids in its foods with the same or slightly greater efficiency (0.97 average) than the chicken *Gallus gallus* (0.90 and higher; McDonald & Morris, 1985).

The estimated Namaqua sandgrouse energy budgets (Table 4) suggest that daily energy budgets in winter are greater than those in summer, due to the increased costs of heat generation for thermoregulation in the colder winter temperatures. Nesting increases energy expenditures by up to 14%. The daily seed intakes needed to meet even the increased energy demands of nesting and egg production are relatively small (7.49–13.73 g day⁻¹; Table 6). The average crop contents of birds collected in the late afternoon (8.24 g; Table 3) will often be enough to meet these energy demands, even when the quantity of seeds emptied from the crop during the day's feeding is not included. A bird will generally consume just enough of the limiting nutrient in its food in order to grow and/or reproduce at its potential (Emmans, 1989). The real possibility that birds are consuming more than they need to balance the requirement for the most limiting nutrient suggests one of three things: (1) their basic requirements have been underestimated, (2) the birds are eating more to build up their nutrient stores, or (3) they are eating more in order to meet the requirements of a nutrient (such as a mineral) that has not been measured in this study. An underestimate of the amount of time spent flying, resulting in an underestimate of requirements, may account for much of the difference, but only more definitive studies will be able to resolve this issue. Estimated daily energy demands for females during the approximately 10-day egg-production period increase by 24–34%, translating to an additional daily seed intake of 1.89–2.64 g (Table 6).

Comparing the estimated daily seed intakes required to meet the demands for the most limiting nutrients during the egg-laying period to the crop contents at the end of a day's feeding suggests that Namaqua sandgrouse are easily able to satisfy these demands during periods of food abundance, but may be nutritionally challenged during periods of food scarcity. Only birds collected after widespread rainfall (Langberg on 22 March 1995; Table 3), when the food supply is expected to reach critically low levels (Wiens & Johnston, 1977), had markedly lower crop contents. Without knowledge of crop-emptying times in sandgrouse, i.e. the quantity of seed that is collected but emptied from the crop during the day's feeding, it is difficult to evaluate to what extent the birds are able to satisfy their nutritional needs at such times.

The Gompertz growth model fitted the average pin-tailed sandgrouse growth data with reasonable accuracy, although the estimated age at maturity (224 g) was considerably lower than the 290 g average weight of adults. This latter result is probably due to the lack of continuous growth data after the age of 53 days. A 1-day old Namaqua sandgrouse chick and an approximately 2-month old female Namaqua sandgrouse that were collected weighed 7.0 g and 125 g, respectively. These values correspond well with the weights estimated by the Gompertz model for Namaqua sandgrouse at similar ages (Table 5).

For a 19-day old Namaqua sandgrouse chick, amino acids are almost certainly more limiting than energy in all the non-legume seed species analysed (Table 7). Energy may

be first limiting in protein seeds, due to the high amino acid concentrations in these seeds. Feathers contain unusually high concentrations of cyst(e)ine (Table 1), and the energetic efficiency of feather synthesis may be as low as 5–20% (Murphy & King, 1992). Chicks grow feathers for a juvenile plumage during their first month, and then undergo a rapid moult into an adult plumage between the ages of 1 and 3 months (Lloyd *et al.*, in press *c*). There is, therefore, a strong possibility that the dietary requirement for methionine will increase to compensate for deficiencies in cyst(e)ine during this period. These results suggest that growing sandgrouse chicks are more dependent on the protein-rich seeds of legume plants to provide them with their most limiting nutrients than are adult sandgrouse.

The dietary requirements for amino acids in a 19-day old chick are similar to those of a female producing eggs (Table 7). However, a chick of this age is approximately one quarter of the weight of an adult female and cannot fly. It will, therefore, be unable to forage for as much food as an adult. Chick development can thus be regarded as probably the most nutritionally demanding stage in the annual cycle of Namaqua sandgrouse. It is surprising, then, that Namaqua sandgrouse in many regions of South Africa time the breeding season in such a way that the chicks are often present during times of lowest food availability (Lloyd *et al.*, in press *a*). In such cases, the timing of breeding may be more dependent on the need to avoid very high nest predation rates (average nest predation of 91% over 4 consecutive years; Lloyd *et al.*, in press *c*) during winter than on nutritional requirements for breeding (Lloyd *et al.*, in review). These results do not support the prevailing assumption (*cf.* Wiens & Johnston, 1977) that granivorous birds require especially large daily seed intakes during breeding if they do not obtain protein from other food sources, such as insects. They do, however, highlight the importance of feeding selectively on protein-rich seeds in such instances.

We thank Dekker and Sikkie Stadler and Hendrik and Lientjie Maritz for their generous hospitality and field assistance to P.L. We are grateful to Shelley Hinsley for permission to use her growth data on pin-tailed sandgrouse and for her comments on an earlier draft. Sue Milton assisted with the identification of plant specimens. We thank Carlos Bosque and an anonymous referee for comments to improve the manuscript. The study was supported by the African Gamebird Research, Education and Development Trust, De Beers Consolidated Mining Company Ltd, and grants from the foundation for Research Development.

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